

First reports of the genus *Nigrobaetis* Novikova & Kluge (Ephemeroptera: Baetidae) from Madagascar and La Réunion with observations on Afrotropical biogeography

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First reports of the genus *Nigrobaetis* Novikova & Kluge (Ephemeroptera: Baetidae) from Madagascar and La Réunion with observations on Afrotropical biogeography. - *Nigrobaetis colonus* sp. n. and *Nigrobaetis cryptus* sp. n. are described from La Réunion and from Madagascar, respectively. This is the first report of the genus from either island and is the first description of a mayfly from La Réunion. These amazing discoveries are of biological importance for the understanding of colonisation processes of the islands in the Western part of the Indian Ocean. The first record of mayflies from La Réunion, a young (<3My) volcanic island, proves the potential of mayflies to disperse over long distances. Recently, *Nigrobaetis bethunae* Lugo-Ortiz & de Moor, 2000 was described from southern Africa (from the border between Namibia and Angola); new reports from eastern South Africa are provided, which greatly extend the distribution range of this species.

Keywords: Baetidae - *Nigrobaetis* - new species - systematics - biogeography - Madagascar - La Réunion - southern Africa.

INTRODUCTION

Nigrobaetis Novikova & Kluge originally was considered to be a subgenus of *Baetis* Leach, and included most of the species of the *Baetis niger* group (Müller-Liebenau, 1969; Novikova & Kluge, 1987). It was thereafter raised to generic level and redefined (Waltz *et al.*, 1994). Despite the apparent similarities between the different species encompassed in this genus, few relevant features were used to characterize the genus. Waltz *et al.* (1994) proposed the following larval characters: body cylindrical, protheca normal or reduced, glossae with few to many dorsal setae, femoral villopore absent, claws without preapical setae. Lugo-Ortiz & de Moor (2000) considered the presence of a small interantennal carina as a generic character, despite the fact that Waltz *et al.* (1984) did not refer to it and that this character is not mentioned in the original descriptions (Soldán, 1977; Müller-Liebenau, 1984; Kang *et al.*, 1994). Other

characters that seem constant in the different species, such as the two kinds of peculiar setae of the distal margin of the labrum, the truncated third segment of the labial palp, the few stout setae between prostheca and mola on both mandibles and the humped posture of the prothorax, were not included in the generic diagnosis. The presence or absence of hindwing pads, as well as the number of gills, are used for specific diagnoses (Lugo-Ortiz & de Moor, 2000). There are no useful characters for separating *Nigrobaetis* from other related genera at the imaginal stage (Waltz *et al.*, 1994).

The genus *Nigrobaetis* comprises 15 species, mainly from the Palearctic (6 species) and Oriental realms (6 species) [terrestrial zoogeographical regions as defined by Zwick (2003)]. The recent description of a species from the Afrotropical realm greatly extended the known range of the genus (Lugo-Ortiz & de Moor, 2000). The simultaneous discovery of the genus on Madagascar and La Réunion is even more surprising. A recent survey of the Malagasy freshwater macroinvertebrates included sampling of more than 650 localities all over the island (Elouard & Gibon, 2001). Based on this material, a study of the systematics of the Malagasy Baetidae increased the known Malagasy Baetidae fauna from eight species belonging in three genera to 54 species in 22 genera (Gattolliat & Sartori, 2003). Despite this intensive research, the genus *Nigrobaetis* was not known to occur on Madagascar. It was only during more recent research on the impact of deforestation on macroinvertebrate community composition that larvae of *Nigrobaetis* were collected in Madagascar.

Ephemeroptera were first found on La Réunion when Starmühlner's expedition collected larvae from two streams (Starmühlner, 1979). The occurrence of insects with low powers of dispersal on an isolated volcanic island of recent origin remains a biogeographical riddle. The Baetidae are the only mayfly family that has been found on this island. The identification of the genus and of its phylogenetic affinity is important for the understanding of the mechanism of dispersion and colonisation of the different islands of the western part of the Indian Ocean. McCafferty & Mauremootoo (2001) tentatively associated the larvae with the genera *Afrobaetodes* Demoulin or *Acanthiops* Waltz & McCafferty. The study of the original material collected by Starmühlner's expedition, as well as other specimens collected by the ORE (Organisme Réunionnais des Eaux) and Christian Guillermet, now allow the assignment of all mayflies living in running waters from La Réunion to the genus *Nigrobaetis*.

Larvae of *Nigrobaetis bethunae* were collected from the Limpopo and Incomati basins in and around the Kruger National Park, South Africa. This constitutes the first report of the species after its description. It greatly enlarges the previously known distribution range, which was restricted to the Cunene River, ca. 2500 km distant on the border between Angola and Namibia. The investigation of this new material adds further information to the original description, especially concerning the larval colouration.

As the examined material from Madagascar and La Réunion differs from all the previously described species, two new species are described here. The holotypes and part of the paratypes are housed in the Museum of Zoology, Lausanne, Switzerland. Other paratypes are deposited in the Museum National d'Histoire Naturelle, Paris (France) and in the Natural History Museum of Vienna (Austria).

DESCRIPTIONS

Nigrobaetis colonus sp. n.

Figs 1-11

MATERIAL EXAMINED

Holotype: 1 larva. La Réunion; Tributary of Marsouin River, Ravine Mathurine (road to Takaka) (F/Ré/9b), 8.04.1974. Leg. F. Starmühlner.

Paratypes: 2 larvae same data as for holotype. 2 larvae, La Réunion; tributary of Marsouin River, Ravine Mathurine (road to Takaka) (F/Ré/9c) 8.04.1974. Leg. F. Starmühlner. 1 larva, La Réunion, Galets River, Amont de la Prise, 7.02.1995. Leg. ORE (Organisme Réunionnais des Eaux). 2 larvae, La Réunion, Marsouin River, Bébou, 10.1996. Leg. ORE.

LARVA

Maximum length: body 5.2 mm; cerci 2.8 mm; median caudal filament 1.8 mm.

Head. Uniformly medium brownish yellow with vermiform marks on vertex and frons. Antennae close to each other, with a small interantennal carina.

Dorsal surface of labrum (Fig. 1) with about nine simple stout setae in the distal half and about six small fine setae in the proximal half; ventral surface with four small pointed setae near lateral margin; distal margin fringed with two kinds of setae: the seven lateral ones long and strongly feather-like and the median ones shorter and only slightly feather-like.

Hypopharynx (Fig. 2): lingua covered with minute stout setae, superlingua with thin setae apically.

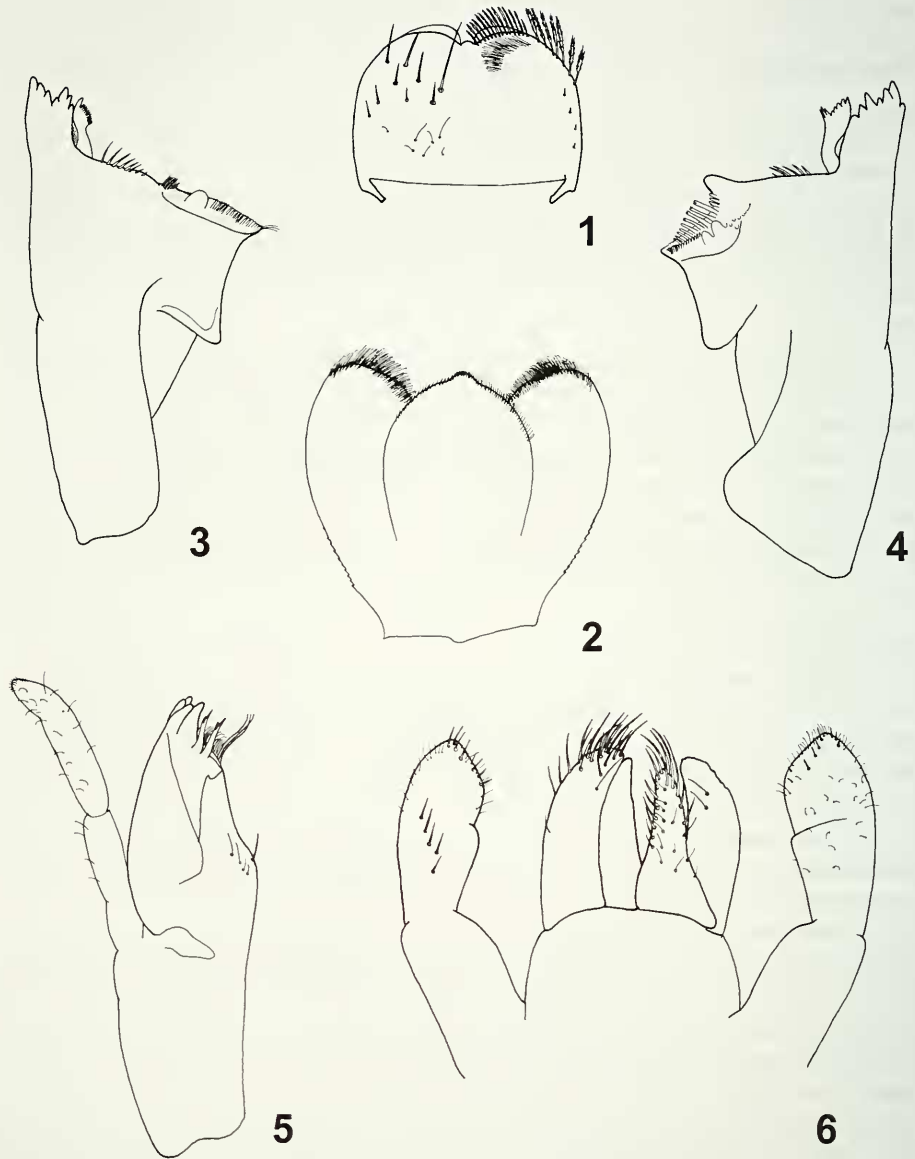
Right mandible (Fig. 3) with two very approximated incisors, outer incisor with three cusps, inner one with four cusps, outer margin straight; very thin setae in proximal half of inner margin of incisors; prostheca with one apical elongated denticle and thirteen short and slender denticles; tuft of few stout setae between prostheca and mola; tuft of setae at apex of mola reduced to two or three setae.

Left mandible (Fig. 4): incisors with seven cusps, outer margin straight; prostheca with five broad denticles and a comb-shaped structure; tuft of a few stout setae between prostheca and mola; tuft of setae at apex of mola absent.

Maxillae (Fig. 5) with four broad teeth, one of them clearly separated but not opposed to others; two rows of setae, the first one formed by abundant small setae ending with three to five setae twice as long as the others, and the second by two long stout spine-like setae; row of four stout setae at base of galea; one single stout seta perpendicular to margin of galea; palp two-segmented with a few thin setae especially at the apex of the second segment, segment 1 approximately 0.8 x length of segment 2, second segment apically clearly turned outward.

Labium (Fig. 6) with glossae slightly shorter than paraglossae; margins of glossae with stout setae increasingly longer towards apex, dorsally with about ten thin setae; paraglossae falcate, with long and stout setae; labial palp three-segmented; segment 1 subrectangular, 0.8 x length of segment 2 and 3 combined; segment 2 with a dorsal oblique row of five long pointed setae; segment 3 truncated, with thin setae more abundant apically and few small pointed setae apically.

Thorax. Thorax uniformly medium brownish yellow without any pattern. Pro- and mesothorax rounded, giving the larva a humped posture in lateral view. Legs yellow except for brownish yellow apex of femora.



FIGS 1-6

Larval structures of *Nigrobaetis colonus* sp. n.: 1: labrum (left : ventral view; right: dorsal view). 2: hypopharynx. 3: right mandible. 4: left mandible. 5: left maxilla. 6: labium.

Forelegs (Fig. 7). Femora dorsally with one row of nine long and pointed setae, without another row of setae subparallel to dorsal margin, dorsoapical setal patch formed by 2 stout setae; ventral margin with stout pointed setae; anterior face almost bare.

Tibiae with only very thin setae dorsally; ventral margin with a few small pointed setae; tibiopatellar suture and subproximal arc of setae absent.

Tarsi with only very thin setae dorsally; ventral margin with few small pointed setae; tarsal claws (Fig. 8) hooked and slender, with one row of about fifteen acute teeth increasing in length toward the apex.

Hindwing pads absent.

Abdomen. Tergal coloration brownish yellow without any pattern. Texture of terga as in Fig. 21.

Sterna brownish yellow, with scales and scale bases; posterior margin without spination.

Gills on segments 1 to 7, elliptic with serrated margin in distal half; tracheation reduced to a central vein (Fig. 10); first gill half the length of other gills, without tracheation (Fig. 9); gill 7 similar to gills 2 to 6.

Paraproct (Fig. 11) with very few scale bases, margin with about six long pointed teeth and a few small ones; postero-lateral extension with a few scale bases, margin with numerous slender teeth.

Cerci and median caudal filament yellow without dark band or annulation, abundant thin setae on inner margins.

IMAGOS

Unknown.

ETYMOLOGY

The specific epithet "colonus" is a Latin noun, meaning "pioneer that colonises a new area".

ECOLOGY

Based on Starmühlner's notes, larvae of *Nigrobaetis colonus* sp. n. were collected in low to medium water currents (0.50 to 1 m/s) in small streams (1 to 2 m wide and 0.05 to 0.2 cm deep) (Starmühlner, 1979). The temperature of the water was 18°C (at 12h) and the pH 7.85. The larvae were not abundant anywhere.

Nigrobaetis cryptus sp. n.

Figs 12-22

MATERIAL EXAMINED

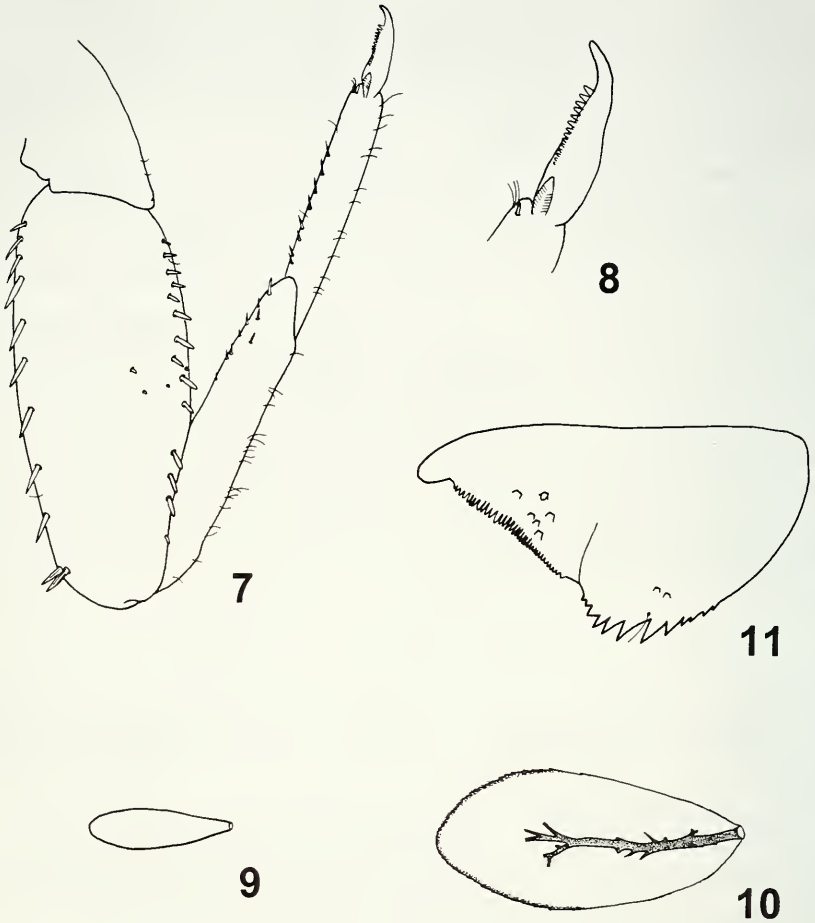
Holotype: 1 larva, Madagascar, Rianila Basin, tributary of Sahatany River. Antanambotsira (near Andasibe), 48°25'49" E, 18°52'53" S, 950 m, 21.02.2002. Leg. R. Oliarinony.

Paratypes: 3 larvae, same locality as for holotype, 22.05.2001. 2 larvae, same locality, 14.09.2001. 2 larvae (1 larva on slide), same locality, 30.11.2001. 6 larvae, Madagascar, Rianila Basin, tributary of Sahatandra River, Madiofasina (near Andasibe), 48°26'33" E, 18°55'23" S, 870 m, 13.06.2001. Leg. R. Oliarinony. 9 larvae, same locality, 14.05.2002. 5 larvae, same locality, 11.09.2001. 2 larvae, same locality, 09.10.2001. 3 larvae, same locality, 13.11.2001. 19 larvae (1 larva on slide), same locality, 27.11.2001.

LARVA

Maximum length: body 2.9 mm; cerci and median caudal filament broken.

Head. Uniformly medium brownish yellow without vermiform marks on vertex and frons. Antennae close to each other, with a small interantennal carina.



FIGS 7-11

Larval structures of *Nigrobaetis colonus* sp. n.: 7: foreleg. 8: tarsal claw. 9: first gill. 10: fourth gill. 11: paraproct.

Dorsal surface of labrum (Fig. 12) with about six simple stout setae in the distal half and about five small fine setae in the proximal half; ventral surface with four small pointed setae near the lateral margin; distal margin fringed with two kinds of setae: the nine lateral ones long and strongly feather-like and the median ones shorter and slightly feather-like.

Hypopharynx (Fig. 13): lingua with minute stout setae apically, superlingua with thin setae apically.

Right mandible (Fig. 14) with two very approximated incisors, outer incisor with three cusps, inner one with four cusps, outer margin expanded and curved; very thin setae in proximal half of inner margin of incisors; prosthema with about nine denticles, the median ones longer than the others; tuft of few stout setae between prosthema and mola; tuft of setae at apex of mola.

Left mandible (Fig. 15): incisors with seven cusps, outer margin expanded and curved; prostheca with five broad denticles and a comb-shaped structure; tuft of few stout setae between prostheca and mola; no tuft of setae at apex of mola.

Maxillae similar to Fig. 5.

Labium (Fig. 16) with glossae slightly shorter than paraglossae; margins of glossae with stout setae, slightly longer apically, dorsally with about seven medium setae; paraglossae apically flattened, with long and stout setae; labial palp three-segmented; segment 1 subrectangular, 0.9 x length of segment 2 and 3 combined; segment 2 with a dorsal oblique row of three long and pointed setae; segment 3 truncated, with thin setae more abundant apically and few small pointed setae apically and ventrally.

Thorax. Brown with a broad central yellow spot, distal part of forewing pads yellow. Pro- and mesothorax rounded, giving the larva a humped posture in lateral view. Legs yellow.

Forelegs (Fig. 17). Femora dorsally with one row of eleven long and pointed setae, without another row of setae subparallel to dorsal margin, dorsoapical setal patch formed by two stout setae; ventral margin with stout pointed setae; anterior face bare.

Tibiae without setae dorsally; ventral margin with a few small pointed setae; tibiopatellar suture and subproximal arc of setae absent.

Tarsi without setae dorsally; ventral margin with seven small pointed setae; tarsal claws (Fig. 18) hooked and slender, with one row of about eleven acute subequal teeth.

Hindwing pads absent.

Abdomen. Terga 1-5 uniformly yellow, terga 6 and 7 brown, tergum 8 brown in proximal third and yellow in distal two thirds, terga 9 and 10 yellow. Terga with scales and scales bases; posterior margin with triangular spines (Fig. 21).

Sterna 1-5 yellow, 6 and 7 brown, 8 and 9 yellow; with scales and scales bases; posterior margin without spination.

Gills on segments 1 to 7, all elliptic with serrated margin in distal half; tracheation generally absent (Fig. 20), only present in some mature larvae (Fig. 19), gill 1 as in Fig. 9.

Paraproct (Fig. 22) with abundant scale bases, margin with about seven long pointed teeth and a few small ones; postero-lateral extension with abundant scale bases, margin with about fifteen teeth.

Cerci and median caudal filament broken.

IMAGOS

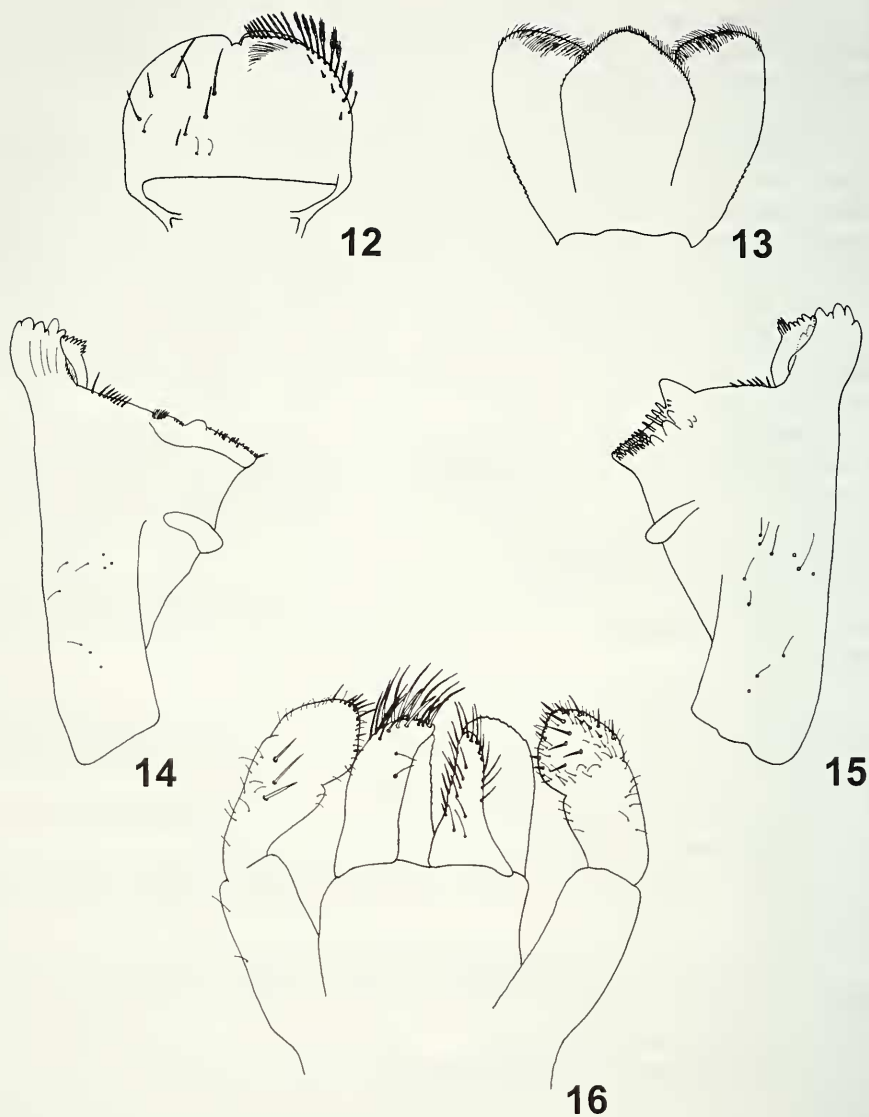
Unknown.

ETYMOLOGY

The specific epithet "cryptus" is a Greek adjective meaning "hidden, the existence of which remains unknown".

ECOLOGY

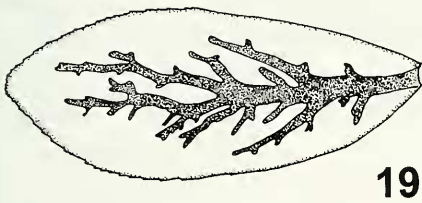
The larvae were collected in two small streams (2-3 m wide and 0.15 m deep) with slow water currents (0.3 m/s) on the Eastern Coast of Madagascar. The water temperature ranged between 16°C and 23.5°C (seasonal variations) and the pH between



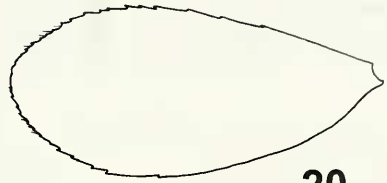
FIGS 12-16

Larval structures of *Nigrobaetis cryptus* sp. n.: 12: labrum (left: ventral view; right: dorsal view). 13: hypopharynx. 14: right mandible. 15: left mandible. 16: labium.

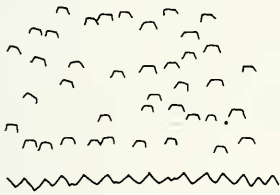
6.8 and 7.3. The substratum component was mainly cobbles and gravel. Despite intensive prospecting in this area, larvae were not collected at any other locality. As the samples were taken every month during a whole year, observation of the larval development indicates that the species is bivoltine, with one generation in June and one in December, at least at these two localities.



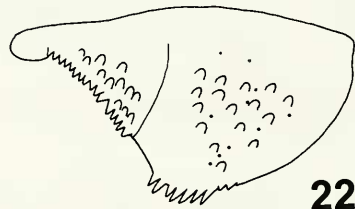
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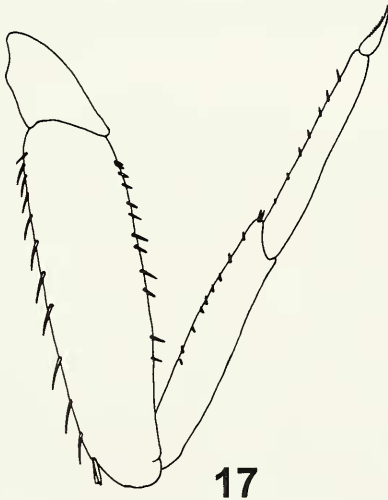
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17



18

FIGS 17 - 22

Larval structures of *Nigrobaetis cryptus* sp. n.: 17: foreleg. 18: tarsal claw. 19: third gill (mature larva). 20: fourth gill (young larva). 21: posterior margin of fourth tergum. 22: paraprot.

Nigrobaetis bethunae Lugo-Ortiz & de Moor, 2000

MATERIAL EXAMINED

5 larvae, (S2103), South Africa, Incomati River system, Buffelspruit River, near Carolina (closer to Badplaas), 30°27'02" E, 26°00'06" S, 1260 m, 16.05.2003. 10 larvae, (S2104), South Africa, Limpopo Basin, Crocodile River, Kruger NP- near Malelane, 31°37'04" E,



FIG. 23

Distribution of *Nigrobaetis* in southern Africa and in the western part of the Indian Ocean. Star: *N. colonus* sp. n. Square: *N. cryptus* sp. n. Circle: *Nigrobaetis bethunae* (black: type locality; grey: new localities).

25°23'57" S, 247 m, 17.05.2003. 10 larvae, (S2108), South Africa, Limpopo Basin, Sabie River, Kruger NP- near Skukuza, 32°00'02" E, 25°09'42" S, 130 m, 18.05.2003. 4 larvae, (S2113), South Africa, Limpopo Basin, Sabie River, Kruger NP- near Skukuza Camp, 31°26'16" E, 24°59'16" S, 289 m, 19.05.2003. 2 larvae, (S2114), South Africa, Limpopo Basin, Olifants River, Kruger NP- near Olifants Camp, 31°40'02" E, 24°01'10" S, 189 m, 20.05.2003. 1 larva, (S2118), South Africa, Limpopo Basin, Letaba River, Kruger NP- near Olifants Camp, 31°46'08" E, 23°59'10" S, 163 m, 21.05.2003. 1 larva, (S2128), South Africa, Limpopo Basin, Tshirovha River, near Thohoyandou, 30°23'44" E, 22°48'55" S, 704 m, 25.05.2003. 2 larvae, (S2134), South Africa, Limpopo Basin, Magoebas River, near Tzaneen, 30°02'34" E, 23°49'51" S, 818 m, 27.05.2003.

All specimens collected by: Helen Barber-James (AM: Albany Museum, Grahamstown, South Africa), Ferdy de Moor (AM), Pascale Derleth (EPFL: Ecole Polytechnique Fédérale de Lausanne, Switzerland; MZL: Musée de Zoologie Lausanne, Switzerland), Jean-Marc Elouard (IRD: Institut de Recherche pour le Développement, Montpellier, France), Jean-Luc Gattolliat (MZL), Dominique Holveck (IRD), Michael Monaghan (NHM: Natural History Museum, London, England), Michel Sartori (MZL).

LARVA

See Lugo-Ortiz & de Moor, 2000; additional morphological information given in the following: General colouration brownish grey with yellow pattern. Head brownish grey. Thorax brownish grey with a broad yellow stripe at base of forewing pads; legs yellow with a transverse brown stripe on femora. Most terga brownish grey with a yellow central symmetric yellow comma, terga 4, 8 and 9 uniformly yellow. In light specimen: tergum 2 with a yellow central spot. In dark specimen: most terga completely brownish grey, terga 8 and 9 yellow. Sterna uniformly yellow, except for

laterally brownish sterna in mature larva sterna. Comparison of this material with material from the Cunene River indicates that the colour pattern is both locally and geographically variable.

IMAGOS

Unknown.

DISCUSSION

Larvae of *Nigrobaetis colonus* sp. n. and *N. cryptus* sp. n. differ from those of *N. niger* (Linnaeus, 1761), *N. digitatus* (Bengtsson, 1912) and *N. rhithralis* (Soldán & Thomas, 1983) by the number of gills (7 vs 6 pairs), the absence of hindwings and the absence of stout setae on the dorsal margin of tibiae; from those of *N. aciniger* (Kluge, 1983) and *N. harasab* (Soldán, 1977) by the number of gills (7 vs 6 pairs); from those of *N. bacillius* (Kluge, 1983), *N. gracilis* (Bogoescu & Tabacaru, 1957) and all the Taiwanese species except *N. facetus* (Chang & Yang, 1994) by the absence of hindwings.

Only *N. bethunae*, *N. facetus* and *N. minutus* (Müller-Liebenau, 1984) cannot be easily separated from *N. colonus* sp. n. and *N. cryptus* sp. n. as they have the same number of gills and no hindwing pads. Morphology of these five species is quite similar. The degree of development of the setae between prostheca and mola of the left mandible (Figs 4, 15), the spination of the right prostheca (Figs 3, 14), the small size of the first pair of gills, the absence of a dark band on cerci, the colouration of the abdomen and the size of the mature larva allow *N. colonus* sp. n. and *N. cryptus* sp. n. to be distinguished from the three other species.

N. colonus sp. n. and *N. cryptus* sp. n. can be separated mainly by the shape of the incisors of both mandibles (Figs 3, 4, 14, 15), the shape of the right prostheca (Figs 3, 14), the colouration of the abdomen and the size of the larvae.

BIOGEOGRAPHY

Among the 23 genera of Baetidae occurring in Madagascar, *Nigrobaetis* is the 14th that is present in both Madagascar and Africa. Unlike most others, its distribution is not restricted to the Afrotropical realm but also includes the Palearctic and Oriental realms. With regard to the specific diversity of the genus in the different parts of its distribution area, it is reasonable to assume a Palearctic or Oriental origin. The presence of *Nigrobaetis* in southern Africa and in Madagascar is probably the result of a step-by-step colonisation: northern Africa to southern Africa and finally Madagascar. As has been assumed for other genera (Gattolliat, 2002; Gattolliat & Sartori, 2003), it is likely that the colonisation of Madagascar took place after its break-off from the Gondwanan mainland (ca. 165 My). This implies an overseas colonization of more than 300 km (Fig. 23).

La Réunion is a young volcanic island (ca. 3 My) and the presence of mayflies there implies overseas dispersal. Based on geographical distance, the probable origin of the mayflies should be either Mauritius (200 km) or Madagascar (800 km); the African mainland is 2250 km distant. *Nigrobaetis* is not known from Mauritius despite

the island's longer history (ca. 8 My). The only mayfly larvae recently collected and described from Mauritius belong to the genus *Cloeon* (McCafferty & Mauremootoo, 2001), a genus also present on La Réunion (Starmühlner, 1979). Thus a tentative conclusion is that *Nigrobaetis* colonised from Madagascar; however, its limited distribution on Madagascar and La Réunion, and the poor knowledge of the aquatic invertebrates of Mauritius, suggest that *Nigrobaetis* occurs on Mauritius but has not been collected.

Nigrobaetis bethunae (southern Africa), *N. cryptus* sp. n. (Madagascar) and *N. colonus* sp. n. (La Réunion) are geographically the closest reported members of the genus. This morphological study confirms the affinities among the three species. *Nigrobaetis bethunae* possesses a wide distribution in southern Africa, but is never abundant, and direct colonisation from Africa seems unlikely because of the more than 2250 km distance.

As noted above, *Nigrobaetis colonus* sp. n. is morphologically closely related to species of the Oriental realm [*N. facetus* (Taiwan) and *N. minutus* (Malaysia)]. Because the Baetidae fauna of the Oriental realm remains poorly known, the recorded distribution range of *Nigrobaetis* remains incomplete. The presence of the genus in India or Sri Lanka is not recorded but is possible. However, even if its presence is confirmed, an Oriental origin for La Réunion seems unlikely because of the distance; ca. 3500 km between India and La Réunion.

Considering the present abundance and distribution, common genera should be the most probable candidates for overseas interchanges. In the case of the Comoros Islands, which are also recent volcanic islands, only the common and widespread genera *Labiobaetis* Novikova & Kluge, 1987, *Afroptilum* Gillies, 1990 and *Cloeodes* Traver, 1938 were successful colonists (unpublished data based on the material collected by Starmühlner's expedition). Consequently, why the rare *Nigrobaetis* was able to colonize La Réunion while other abundant and widespread genera did not remains an important question.

In conclusion, the occurrence of *Nigrobaetis* on La Réunion is surprising and the origin of *Nigrobaetis colonus* sp. n. remains unclear, even if an Afrotropical origin is probably the most likely. Is the small size of *Nigrobaetis* part of the explanation of this riddle? Was *Nigrobaetis* once much more abundant in the Afrotropical area than it is at present time? Is this genus perhaps more widespread than it is yet recorded? The question remains open. In clarifying the affinities of *Nigrobaetis colonus* sp. n., molecular phylogenetic studies could greatly help to solve this puzzle and determine the colonizing source. The presence of *Nigrobaetis* on La Réunion indicates successful overseas colonisation of at least 800 km and constitutes the final proof that the dispersal capacities of mayflies are greatly underestimated. It means that colonization over long distances must be taken in account when biogeographical scenarios are established.

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